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Home range and movement patterns of red snapper (*Lutjanus campechanus*) on artificial reefs

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ABSTRACT

Red snapper (*Lutjanus campechanus*) are associated with artificial habitats in the Gulf of Mexico (GOM). However, fine-scale movements and use of artificial reefs by red snapper over diel periods is unclear. Both manual and passive telemetry were used to examine fine-scale movement patterns and residence time of red snapper around artificial habitats to evaluate the importance of these structures to this species. Red snapper (550–745 mm TL; $n = 12$) were manually tracked at artificial reefs in the northeastern GOM over 24-h periods. Fish stayed near the artificial reefs (<100 m, with 75% of locations within 30 m of the structure), but were significantly further from the reefs at night (mean = 27.5 m, SD = 7.1) than day (mean = 19.1 m, SD = 8.2). Based on manual tracking, home range and mean distance from the reef increased with fish size. These fish also showed long term residence of 332–958 d based on passive acoustic monitoring. The close proximity of these fish to the reef over 24-h periods and the long-term residency provides evidence that these artificial reefs are important habitat for red snapper and should be considered an effective management tool.

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1. Introduction

Red snapper (*Lutjanus campechanus*) are one of the most numerically abundant fish species on both natural and artificial habitats off Alabama, USA (Gitschlag et al., 2003; Lingo and Szedlmayer, 2006; Wells and Cowan, 2007; Gallaway et al., 2009). Natural reef habitat is relatively rare in the northern Gulf of Mexico (Parker et al., 1983; Schroeder et al., 1988); however, approximately 10,000–20,000 artificial habitats have been deployed off coastal Alabama and Mississippi to enhance available reef habitat (Minton and Heath, 1998; Szedlmayer, 2007; Gallaway et al., 2009; Shipp and Bortone, 2009). Estimates of red snapper site fidelity to these artificial habitats from mark-recapture and acoustic telemetry methods have differed in previous studies, but in general red snapper showed a close association with these structures (Beaumariage, 1969; Fable, 1980; Szedlmayer and Shipp, 1994; Szedlmayer, 1997; Westmeyer et al., 2007; Szedlmayer and Schroepfer, 2005; Topping and Szedlmayer, 2011). For the most part, these previous movement studies have focused on residence time and site fidelity, while few studies have examined the

fine-scale use of these structures and the adjacent silt-sand habitat (Szedlmayer, 1997; Szedlmayer and Schroepfer, 2005).

Szedlmayer (1997) used acoustic telemetry to relocate red snapper monthly at release sites and adjacent structures. Although most fish showed long-term residence and some movement was detected to other structures 88–700 m from the release site, sampling frequency was inadequate for defining fine-scale diel patterns. One study examined fine-scale movements of red snapper over 9- to 16-h periods, and found that red snapper used small areas (mean = 2314 m²) and stayed relatively close to the reef (mean = 29 m; maximum = 66 m; Szedlmayer and Schroepfer, 2005). They also showed red snapper tended to be closer to the reef at dawn than at dusk or nighttime periods, but day comparisons were not reported and sample size was low ($n = 4$). Westmeyer et al. (2007) used low-resolution (~75 m) remote receivers to continuously monitor small red snapper (<500 mm TL) at oil platforms and found a crepuscular pattern of movement away from the structure.

Diet studies have suggested that red snapper may use different habitats over diel and seasonal periods based on changes in prey availability (Ouzts and Szedlmayer, 2003; McCawley and Cowan, 2007). Diel movements away from the reef at night are probably related to foraging behavior as indicated by diel diet shifts (Ouzts and Szedlmayer, 2003). Collectively, these previous telemetry and diet studies indicated that red snapper may stay relatively close to the reef structure and feed on reef and adjacent open habitat prey types.

Determining the home range areas of red snapper at artificial reefs over diel periods can help clarify the immediate benefits red

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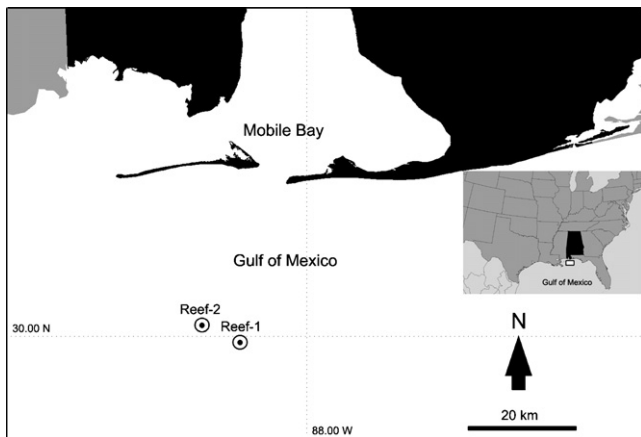
Fig. 1. Locations of reef-1 and reef-2 in the northeast Gulf of Mexico. Inset (right) shows Gulf of Mexico and study area (black box) offshore Alabama (black), USA.

snapper obtain from these structures and adjacent open habitats (Szedlmayer and Able, 1993; Meyer et al., 2000; Lowe et al., 2003; Topping et al., 2005). This information combined with long-term residence data (>1 year) can provide a comprehensive understanding of how fish may use available habitat (Szedlmayer and Schroepfer, 2005; Schroepfer and Szedlmayer, 2006; Topping et al., 2006). In the present study, both long-term telemetry monitoring (>1 year) and short-term, high-resolution manual tracking (24 h; ±5 m) methods were used to assess residence time, home range area and diel movements of red snapper at artificial reefs.

2. Methods

2.1. Study area

The study area was located in the northeastern Gulf of Mexico, 25 km south of Mobile Bay, AL, USA. Red snapper were tagged at two artificial reef habitats: reef-1 was an M-60 army tank (7 m × 3 m) and reef-2 was a steel frame pyramid (5 m × 5 m; Fig. 1). Both reefs were built over open flat sand-mud substrate and were 7 km apart. These reefs were typical public artificial reefs deployed in the Hugh Swingle Reef Permit Area and were at 25 m depths.

2.2. Fish tagging

Large red snapper (>500 mm total length [TL]) were captured at reef-1 and reef-2 with hook and line. Tagging procedures followed Szedlmayer and Schroepfer (2005). Fish were brought on board the research vessel, placed in a 70-L tank of seawater containing MS-222 (150 mg L^{-1}), and quickly anesthetized to level 4 (Summerfelt and Smith, 1990). Once sedated, the fish were temporarily removed from the anesthetic to obtain weights and lengths. A transmitter (Sonotronics CT-05-48, Tucson, AZ; pulse period = 850–1250 ms, 70–83 kHz, 16 mm × 79 mm, life = 4 years) was implanted through a small (18 mm) vertical incision made into the peritoneal cavity with a No. 11 scalpel slightly above the ventral midline and then sutured with plain gut suture (Ethicon, no. 2, 3.5 metric). Also, an internal anchor tag (Floy) was inserted into the incision before it was sutured. Sterile surgical methods and betadine were used throughout the procedure. After surgery, the fish were released after a short, (~1 min) period of recovery at the surface (when fin and gill movements were observed). Fish were released at the capture site by lowering fish to the bottom with a weighted line with an inverted barbless hook that was attached to the fish's lower jaw. Upon retrieval of the weighted line the fish was released at depth near the reef.
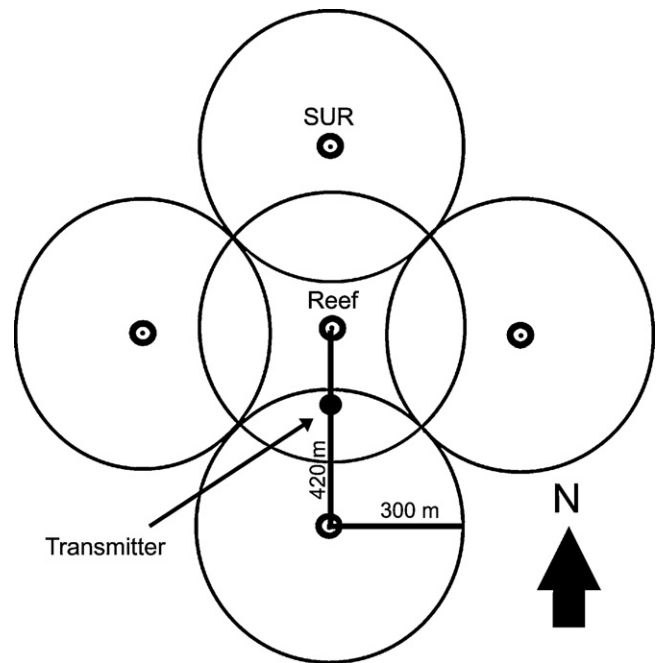
Fig. 2. Receiver array design for each site, with one receiver at the reef and four others surrounding the reef 420 m away to the North, South, East, and West. Circles represent detection range of 300 m. A control transmitter was placed 150 m south of reef.

2.3. Long-term continuous remote monitoring

The presence (or absence) of red snapper within a 1 km radius of the site of release was monitored with underwater acoustic receivers. The transmitters used in these red snapper had a unique frequency (70–83 kHz) and pulse interval (850–1250 ms) code for each fish that was recorded by Sonotronics underwater omni-directional receivers (SURs) deployed at each reef site. At each reef site, five SURs were moored near the bottom (5 m above the substratum), with one receiver located at the center release site and the other four placed 420 m to the North, South, East, and West of the center (Fig. 2). Maximum detection ranges were 600 m for these transmitters based on increasing distances of transmitters away from SURs until they could no longer be detected, but for array design a conservative detection range of 300 m was assumed to ensure detection of emigrating fish. The design of this array allowed detection of all fish within a 1 km radius of the release site based on these preliminary range tests. In addition, a stationary control transmitter was moored 5 m above the bottom at a distance of 150 m south of the center receiver at both reefs. These control transmitters, present throughout the study, were used to detect any reduction in detection range of transmitters due to environmental factors. All receivers were coated with antifouling paint to prevent decreased detections due to biofouling (Heupel et al., 2008).

2.4. Manual tracking

In addition to monitoring the presence of these red snapper within 1 km of these reef sites, these fish were also manually tracked via surface vessel to determine their fine-scale movements around the reef over diel periods. Transmitters used in the present study also transmitted a continuous acoustic "ping" (~1000 ms pulse period) that enabled manual tracking of fish from an 11-m research vessel. The research vessel was fitted with a Vemco V10 directional acoustic hydrophone and a VR60 surface receiver (Holland et al., 1983; Topping et al., 2005). Red snapper were

tracked for multiple, 24-h diel periods around reef-1 and reef-2. Fish were not manually tracked immediately after release to allow for recovery after surgery; fish were tracked after 7–10 months at liberty. Locations of latitude and longitude were recorded at 30-min intervals with a Global Positioning System (GPS) as the boat was positioned over the fish. This method has been shown to provide both the fine-scale temporal and spatial (~5 m) resolution needed for estimates of habitat use over diel periods (e.g. Worton, 1989; Seaman and Powell, 1996; Lowe et al., 2003; Topping et al., 2005). The accuracy of this tracking method was also validated in the present study by recording locations of stationary transmitters during manual tracking periods and comparing these estimated locations to the known locations of stationary control transmitters (mean = 4.98 m, SD = 3.97; n = 7).

2.5. Data analyses

Locations (latitude and longitude) for red snapper obtained from 24-h manual tracking and the location of the artificial reefs were plotted in a Geographic Information System (ArcView GIS, version 3.2a). Area use was calculated with the Animal Movements Analyst Extension (AMAE) in ArcView (Hooge et al., 1999, 2001). To describe each fish's home range a 95% kernel utilization distribution (KUD) was used, i.e., the area that a fish has a 95% probability of being located over the duration of the tracks (Worton, 1989; White and Garrott, 1990; Seaman and Powell, 1996; Topping et al., 2005). A 50% KUD (50% probability polygon) was used to determine each fish's core range. The ad hoc smoothing value (AMAE home range) was used when calculating the KUDs. Analyses of area use were also estimated with minimum convex polygons (MCP) for comparisons to previous studies (Zeller, 1997; Szedlmayer and Schroepfer, 2005). MCP areas were calculated for each individual fish and for all fish combined at each reef. Distances away from the center of the habitat to each location were measured with the distance tool from the AMAE in ArcView GIS. The proportions of all locations were calculated at 10 m intervals from the reef site. Proportions were arcsine-square root transformed and compared among 10 m intervals with a mixed model repeated measures analysis of variance (fixed, 10-m intervals; random, fish; rmANOVA). If significant differences were detected with the rmANOVA, a Tukey multiple comparison test was used to show specific differences among distances (Littell et al., 1998; Cody and Smith, 2006). The effects of fish size (TL) on mean distance from the reef and on log transformed measures of home range size were analyzed with a linear regression (Jones, 2005; Cody and Smith, 2006; Nanami and Yamada, 2008). Since fish were assumed to be larger at the time of tracking (7–10 months after release), regressions comparing fish size to distance from reef were calculated from predicted TL at the time of tracking. Predicted TLs were derived from the Von Bertalanffy curve in Wilson and Nieland (2001). Mean distances from the reef were compared between day and night periods for all fish with a paired t-test (Zar, 1984). Mean distances from the reef for each fish were also examined at 1-h intervals over a 24-h diel cycle. A mixed model (fixed, 1-h periods; random, fish) rmANOVA was used to compare mean distances among 1-h time intervals over 24-h diel periods, followed by a Tukey test to show specific differences (Littell et al., 1998; Cody and Smith, 2006). Bearings were calculated from the center of the reef to fish locations with ArcView GIS (Bearing and Distance Extension 1.1, ESRI script, Ron Schultz, 2003, www.esri.com/arcscripts). Mean bearings were estimated following methods described by Kölliker and Richner (2004). Rayleigh's z-test was used to test for directionality (non-random direction) of locations from the reef (Batschelet, 1981; Kölliker and Richner, 2004). The proportions of locations within 30° intervals (arcs) over a 360° range around the reef were determined for each fish for

visual comparisons. All differences were considered statistically significant at $P \leq 0.05$.

3. Results

Red snapper (n = 12) were both manually tracked for multiple 24-h periods from the surface and monitored continuously with automated receivers (SUR) up to 958 d (Table 1). Mean size was 631 mm TL (SD = 54, range = 550–745 mm TL) and mean weight was 3.7 kg (SD = 1.0). Fish showed long-term residency to the reef sites, and were manually tracked over several 24-h periods after 7–10 months at liberty (Table 1 and Fig. 3). At reef-1, fish 1, 2, and 3 were initially tracked over a 24-h period on 24–25 June 2008; in addition, these fish 1–3 and fish 4–6 were all tracked concurrently (location for each fish every 30 min) for a complete 24-h period on 2–3 July 2008. Additional fish (7–9) were released at reef-1 on 22 October 2008 and tracked on 31 May 2009, along with fish 5. At reef-2, fish 10, 11, and 12 were tracked over a 24-h period on 25 August 2009 (Table 1). All tracking periods were conducted in relatively calm conditions, with winds < 5 m s^{-1}.

All red snapper stayed within a relatively small area that encompassed the artificial reefs during all tracks. Mean home range area estimates with the 95% KUD were 2866 m^2 (SD = 1691) at reef-1 and 6204 m^2 (SD = 4264) at reef-2, while mean core area (50% KUD) was 356 m^2 (SD = 177) at reef-1 and 935 m^2 (SD = 211) at reef-2. The mean 100% MCP area was 2899 m^2 (SD = 1891) at reef-1 and 9499 m^2 (SD = 2526) at reef-2. At reef-1, an area of 1114 m^2 was obtained where each fish's 100% MCP completely overlapped (10% of total MCP area; Fig. 4). At reef-2, the area of overlap was 5149 m^2. For both sites, reef areas were completely within this area of 100% overlap (i.e., the reef site was used by all red snapper tracked). For the fish tracked on 2 July 2008 (fish 1–6), the 95% KUD area significantly increased with fish size; however, the core area and 100% MCP were not significantly affected by fish size. A significant positive linear relation was detected between the log–log transformation of the 95% KUDs and TLs of fish 1–6 (R^2 = 0.73, p = 0.03; $\log_{10}$ [95% KUD] = 2.1384 $\log_{10}$ [TL] − 2.732).

Over all 24-h tracks, all fish stayed close to the reef structure (mean distance = 22.3 m; SD = 7.5; Table 1). About 55% of all fish locations (on average) were within 20 m of the reef sites and 75% were within 30 m of the reef sites (Fig. 5). Mean proportion of fish locations within 0–10 m (25%), 10–20 m (29%), and 20–30 m (21%) were significantly greater than proportions beyond 30 m from the reefs (<10%; rmANOVA: $F_{7,79}$ = 23.08, p < 0.001; Fig. 5). A significant positive relation was detected for fish 1–6 on 2 July 2008 between mean distances from the reef and total length (R^2 = 0.84, p = 0.01; Fig. 6). Trends were similar but not significant for the fish tracked on 31 May 2009 (fish 5, 7–9; R^2 = 0.79, p = 0.11) and 25 August 2009 (fish 10–12; R^2 = 0.91, p = 0.19; Fig. 6). Red snapper (n = 12) mean distances from the reef over 24-h were significantly different between day (mean = 19.1 m, SD = 8.2) and night periods (mean = 27.5, SD = 7.1; Paired t-test: t_{11} = 4.85, p < 0.001; Fig. 4). Only two fish moved further from the reef during the day than at night, both on reef-2 (fish 10, 34 vs. 32 m; fish 12, 28 vs. 31 m). All other fish showed a 4–15 m increase in mean distance from the reef at night than day. Diel differences in mean distance from reefs for 1-h intervals were detected for some hours of day and night, and were consistent with greater distances at night (rmANOVA: $F_{23,251}$ = 4.04, p < 0.0001; Fig. 7). Distances from the reef reached a maximum around 2100–0200 h, where mean distances increased from mid-day to nighttime hours then decreased around sunrise (Fig. 7). Fish (1–6) tracked on 2 July 2008 had locations that were skewed northwards of the reef. Mean bearings of these red snapper were within a north quadrant from 322° to 19° and were significantly different from random (Fig. 8; Rayleigh's z-test: p < 0.02).

Table 1
Summary of telemetry data for red snapper (n = 12) manually tracked for 24-h periods at reef-1 and reef-2. Home range area (m^2) was estimated with the 95% kernel utilization distribution (KUD) and core range by the 50% KUD. Areas were estimated for all fish positions with a minimum convex polygon (MCP). Distance, mean distance (m) of fish positions from the reef; n, number of locations for all tracks; DAL, days at liberty until "event" based on long-term monitor data; event, emigrated (E), caught (C) or present (P) by end of study.

Fish	Site	Date released	Dates tracked	TL (mm)	DAL (d)	Event	n	95% KUD (m^2)	50% KUD (m^2)	100% MCP (m^2)	Distance (m ± SD)
1	Reef-1	29 August 2007	24 Jun 2008 2 July 2008	710	379	E	80	2125	233	1880	17.3 ± 10.8
2	Reef-1	14 November 2007	24 June 2008 2 July 2008	579	464	E	80	1704	218	1631	13.0 ± 7.7
3	Reef-1	05 September 2007	24 June 2008 2 July 2008	635	332	C	79	1906	262	3207	15.0 ± 9.7
4	Reef-1	29 August 2007	02 July 2008	645	339	C	58	2158	446	1325	17.3 ± 11.4
5	Reef-1	29 August 2007	02 July 2008 31 May 2009	550	958	P	58 / 59	1234 / 6993	230 / 1278	1068 / 7506	13.5 ± 8.9 / 27.6 ± 17.6
6	Reef-1	29 August 2007	02 July 2008	601	332	C	58	1421	137	1200	14.5 ± 9.6
7	Reef-1	22 October 2008	31 May 2009	745	382	E	59	5174	522	5105	34.6 ± 16.7
8	Reef-1	22 October 2008	31 May 2009	590	268	C	59	4861	518	5791	23.2 ± 16.1
9	Reef-1	22 October 2008	31 May 2009	645	537	P	59	5208	642	4880	23.0 ± 14.3
10	Reef-2	21 October 2008	25 August 2009	645	595	P	52	8207	1162	8747	33.9 ± 18.0
11	Reef-2	21 October 2008	25 August 2009	610	415	E	52	1307	745	7435	25.5 ± 17.6
12	Reef-2	21 October 2008	25 August 2009	620	384	E	52	9098	897	12,316	30.0 ± 19.8

Long-term monitoring data showed the tracked fish remained relatively close to the sites before and after the tracking periods, and remained resident at the sites from 268 to 958 days after release. The shortest residence times, 332 d at reef-1 and 268 d at reef-2, resulted from fisher removals. Of the 12 fish tracked, four were captured at the release sites, five emigrated, and three were present at the end of the study. Some fish (fish 1, 7, 10) left the site for up to six months, but returned and again showed a close association with the reef sites (Table 1, Fig. 3). None of these fish emigrated between the two sites used in this study, and all fish were captured at the site of release.

4. Discussion

This study was the first to examine fine-scale movements and home ranges of large red snapper (>500 mm TL) around relatively small artificial reefs (i.e., army tanks). Telemetry methods used were successful in detecting even small diel differences in red snapper distances from the reef and were able show long-term residence of these same fish to the reef up to 958 d.

The 24-h manual tracking showed that these large red snapper remained relatively close to the reef structure. Similar short-term movement distances for red snapper (mean = 29 m) were shown for crepuscular and nighttime periods, but were not measured over day periods (Szedlmayer and Schroepfer, 2005). Also, their area use estimates for red snapper with a 100% MCP (1074–3361 m^2) were similar to 100% MCP estimates of the fish tracked at reef-1 (1068–5791 m^2), while fish at reef-2 had larger MCPs (7435–12,316 m^2). At both reefs, the 50% KUD core area estimates were small (137–1162 m^2), but all fish's core areas and 100% MCP overlapped the reef structures. The total inclusion of the reef structure within these core areas demonstrates the importance of these structures to red snapper over daily periods.

Red snapper were continuously detected during the 24-h tracking periods, implying that red snapper did not move inside the army tank structure (reef-1) for extended periods of time, i.e., such movements would have caused a complete loss of detection (Bradbury et al., 1995; Giacalone et al., 2005; Topping et al., 2005, 2006). Red snapper will on occasion move inside and underneath the army tank structures, as directly observed during daytime SCUBA surveys (Authors, personal observation). Reef-2 was a steel pyramid and did not have enclosed compartments that would have blocked signal transmission.

One other study that did examine fine-scale movement patterns of red snapper, manually tracking fish over 9- to 16-h periods, showed that red snapper stayed relatively close to the reef (mean = 29 m; maximum = 66 m; Szedlmayer and Schroepfer, 2005), which is similar to the results in the present study (mean = 22 m) for fish tracked over 24-h periods. In this study, fish
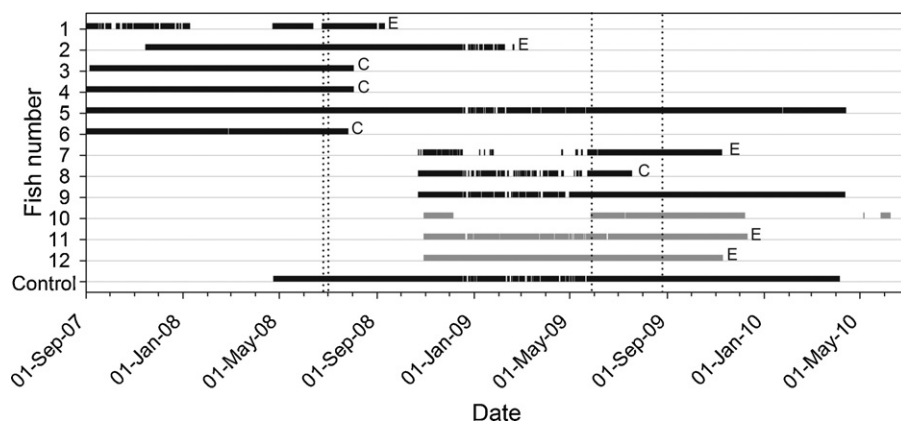

Fig. 3. Daily presence of red snapper (n = 12) and detection of stationary transmitter (control) at reef-1 (black) and reef-2 (gray). Vertical dashes represent dates a fish was present (i.e., detected at least five times by any receiver). Letters at end of record indicate events (C, caught; E, emigration; no letter, present at end of study). Vertical dotted lines show dates of 24-h manual tracking.
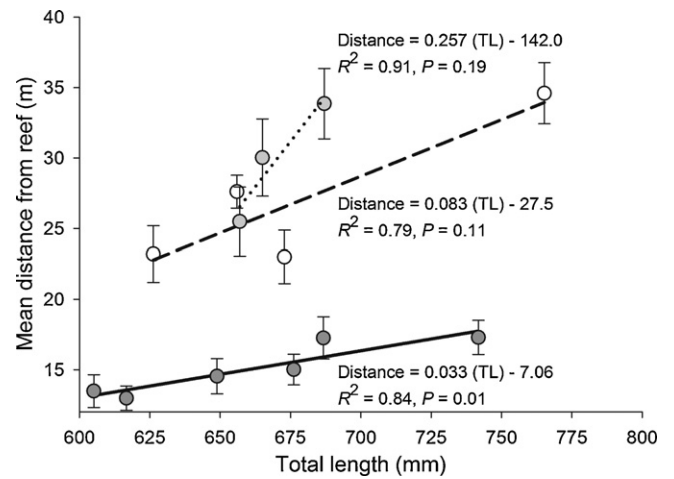
Reef-1

Reef-2

50 m
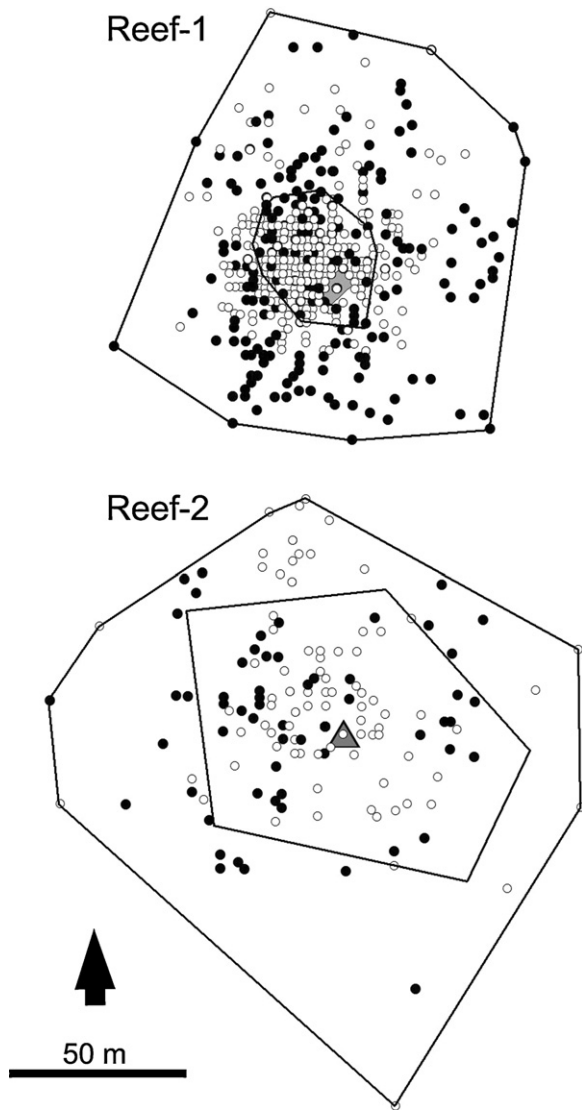
Fig. 4. Day (open circles) and night (solid circles) locations of red snapper at reef-1 (n = 9; gray rectangle, army tank) and reef-2 (n = 3; gray triangle, pyramid) over all 24-h tracks. Outer polygon = 100% MCP for all fish locations. Inner polygon, area of 100% overlap of 100% MCPs for each fish.
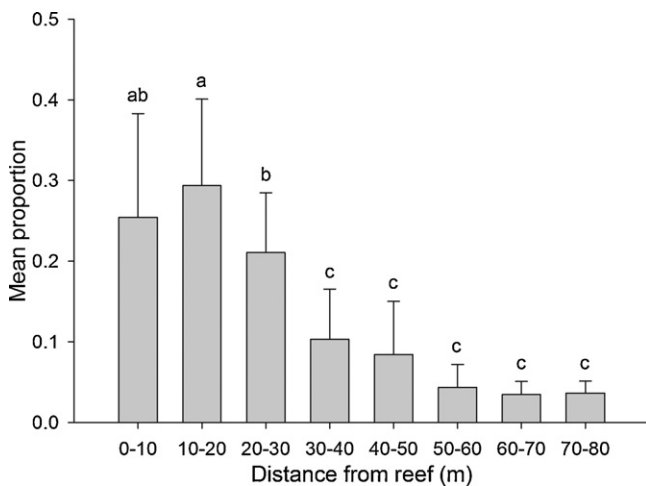
Fig. 5. Mean proportion (+SD) of red snapper (n = 12) manual tracking locations within 10-m distance bins from the center of the reef. Different letters indicate significant differences between an arcsine-square root transform of actual proportions shown (P < 0.05).

Distance = 0.257 (TL) − 142.0
R^2 = 0.91, P = 0.19

Distance = 0.083 (TL) − 27.5
R^2 = 0.79, P = 0.11

Distance = 0.033 (TL) − 7.06
R^2 = 0.84, P = 0.01

Fig. 6. Relation between red snapper total length (TL) and the mean distance (±SE) fish were located from the center of the reef over all 24-h tracks. Dark gray circles represent fish tracked on 2 July 2008 (n = 6), open circles are fish tracked on 31 May 2009 (n = 4) and light gray are fish tracked on 25 August 2009 (n = 3). Total lengths (TL) were adjusted to reflect predicted size on tracking date (Wilson and Nieland, 2001).

at reef-2 had a greater mean distance from the reef than fish at reef-1, which may have resulted from tracking fish on different dates. Differences in movements (mean distance from reef) of fish tracked at reef-1 were greater among different dates than among fish (fish 1–6 vs. 7–10; Table 1). However, movements can also be affected by the complexity of structures within a fish's home range, e.g., graysby (*Cephalopholis cruentata*) spent more time in areas with high rugosity (Popple and Hunte, 2005). Red snapper may have been more closely associated with the more complex habitat of reef-1 compared to reef-2.

Szedlmayer and Schroepfer (2005) reported maximum distances up to 66 m, which is similar to results of the present study (maximum = 100 m). Differences in mean overall distances and diel distances red snapper moved from the reef may reflect changes in prey availability (Ouzts and Szedlmayer, 2003; McCawley and Cowan, 2007). Red snapper may move greater distances away from structures due to increased competition for food resources. If true, red snapper movements away from oil platforms (greater
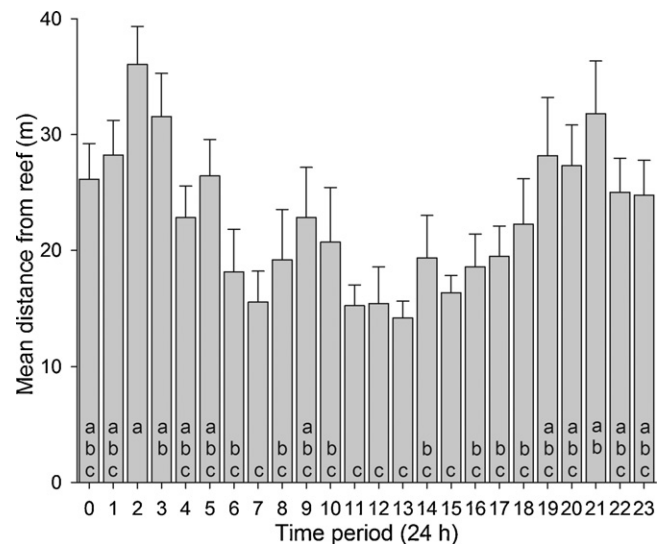
Fig. 7. Red snapper (n = 12) mean distance (+SD) from the center of the reef sites over diel periods (0000–2300 h; i.e., 0–23 h) for all 24-h tracks. Time periods with different letters indicate significantly different mean distances (P < 0.05).
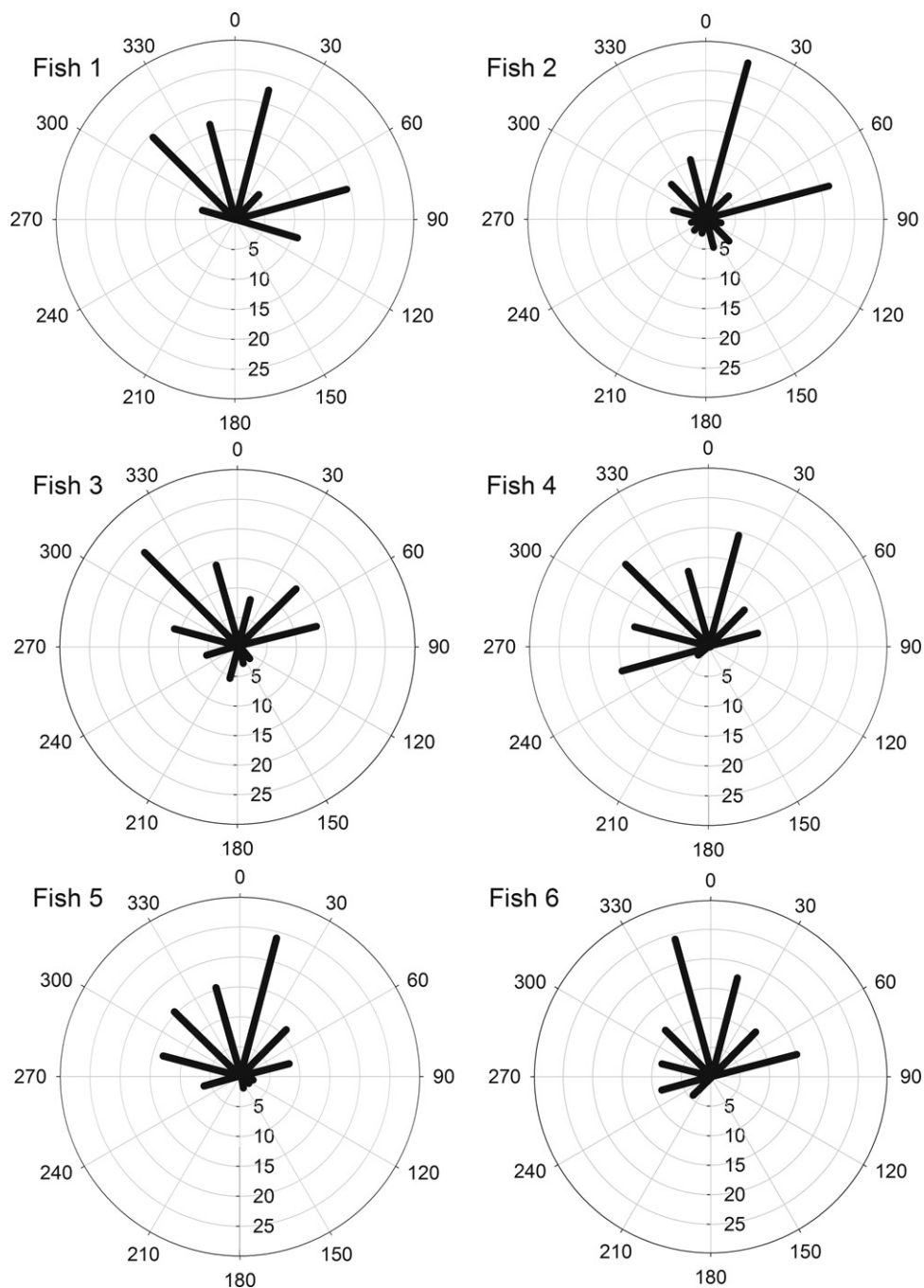
Fig. 8. Compass plots for each red snapper ($n = 6$) showing the percentage of locations within each 30° arc around the center of reef-1 from 24-h manual tracks on 2 July 2008. North is 0°.

numbers of red snapper and other species) would be greater than the smaller artificial reefs in the present study (Turpin and Bortone, 2002; Gitschlag et al., 2003; Lingo and Szedlmayer, 2006).

Intraspecific differences in home range size and distances fish move on a daily basis have been attributed to body size (Jones, 2005; Topping et al., 2005; Nanami and Yamada, 2008), reef shape (Zeller, 1997; Eristhee and Oxenford, 2001; Popple and Hunte, 2005; Topping et al., 2005), and habitat availability (Matthews, 1990). A positive relation between home range size and fish size may be influenced by the greater resource demand of larger fish, and this relation can vary by trophic feeding level (i.e., carnivore vs herbivore; Brett, 1965; Harestad and Bunnell, 1979; Wakeman et al., 1979; Jones, 2005; Topping et al., 2005; Nanami and Yamada, 2008). In the present study, a positive relation was detected even though

there was a small size range of tracked red snapper (550–745 mm TL). Based on the present relation of fish size and movements, little movement for red snapper $\leq$100 mm TL would be expected, and a home range of 35 m^2 would be obtained from the log–log relation (i.e., $\log_{10}$ [home range] = 2.138 $\log_{10}$ [TL] − 2.732). In contrast, Chapin et al. (2009) showed greater movement for smaller snapper (mean = 110 mm TL), with observed movements up to 206 m from release sites over 243 d, thus a fine-scale movement study of smaller size classes is needed for comparisons of fish size to daily movement patterns. In addition, Gallaway et al. (2009) suggested that smaller younger red snapper were more inclined to show greater movements due to competitive exclusion of larger older conspecifics. Interestingly, positive relations between fish size and distance from reef were found across red snapper tracked over the

same 24-h period. However, greater variability in fish movements among tracking dates (even for the same fish) apparently masked any relation between fish size and their distance from reef when comparing all fish. This pattern would suggest that at daily scales fish size may be an important factor in movements, but there are other underlying factors affecting area use on seasonal scales. Variability in area use was lower between temporally close tracking dates (weeks vs years), which suggests that seasonal changes in prey availability or another seasonally variable factor may be an important in controlling movement patterns.

Nanami and Yamada (2008) estimated home range sizes of 93–3638 m^2 for the checkered snapper (*Lutjanus decussatus*) over various size ranges (100–250 mm TL) on a shallow (2 m) fringing reef. A relation of home range size to body size (TL) was also detected for checkered snapper even though fish were smaller than red snapper tracked in the present study. These home range sizes of checkered snapper were similar to red snapper in the present study on what would be considered a "patch reef" in other studies (e.g., Zeller, 1997). Meyer et al. (2007) detected much greater movements for the larger (520–890 mm fork length) green jobfish, (*Aprion virescens*) tracked with remote receivers deployed along fringing reefs. Green jobfish showed movements along these fringing reefs up to 24 km over diel periods, with regular diel shifts in area use up to 9 km. These studies suggest that red snapper may show greater movements on natural reef types where the structure covers a larger area or has an elongated shape, such as a fringing reef. Topping et al. (2005) showed significantly greater home range sizes (1930–82,070 m^2) for the California sheephead *Semicossyphus pulcher* tracked along a elongated, rocky coastline relative to the same species tracked in an embayment (554–850 m^2), and movement was related to foraging and nighttime resting habitats over diel periods. Within these same habitats, kelp bass *Paralabrax clathratus* tracked at Catalina Island had smaller home ranges (33–11,224 m^2) than California sheephead, and these differences were attributed to their diet (Lowe et al., 2003; Topping et al., 2005). Red snapper diets change ontogenetically, seasonally, and over diel periods (Ouzts and Szedlmayer, 2003; Szedlmayer and Lee, 2004; McCawley and Cowan, 2007), and differences in movement patterns may reflect changes in prey availability at different habitats (Matthews, 1990). The small home ranges of each red snapper that encompassed the reef structures in the present study would suggest that artificial reefs and adjacent mud-sand habitat can provide the daily resources (food and shelter) that this species requires within a relatively small area.

It was unclear what caused the skewed northward movement patterns of red snapper around the artificial habitat for fish tracked on 2 July 2008. These fish were located on all sides of the reef at some point during the tracking, but locations were skewed to the north side of the reef. Water currents have been found to affect the location of fish on reefs and may affect prey distribution (Kingsford and MacDiarmid, 1988; Webster and Hixon, 2000). Accurate current directions and speeds were not measured in the present study, but should be considered in future studies of red snapper movement patterns.

The long-term data from the present study showed some red snapper remained within ~1 km of the reef (based on detection range) up to 958 d (n = 8) with occasional periods spent outside detection range, some fish were removed from the release site prematurely by fishers (n = 4) after 268 d, and one moved during hurricanes after 379 d. Long-term telemetry data for red snapper in other studies have shown similar residence times at artificial habitats (Szedlmayer and Schroepfer, 2005; Schroepfer and Szedlmayer, 2006; Topping, 2009; Topping and Szedlmayer, 2011). These previous studies showed red snapper occasionally moved greater distances (excursions and relocations) compared to movements measured on a daily basis in the present study; however, in those studies, fish would be resident on one habitat for extended periods then quickly move to another habitat and would again take up residence (Topping and Szedlmayer, 2011). It is suggested that while red snapper were resident on a particular site they would show home ranges and movement patterns similar to red snapper in the present study. Diel movements, especially away from the reef at night, are probably related to foraging behavior as indicated by diel diet shifts shown in previous studies (Ouzts and Szedlmayer, 2003).

Overall, this study showed that artificial reefs and nearby areas (<100 m) provided suitable habitat for red snapper over a wide range of temporal and spatial scales. The short distances fish moved from the reef in this study indicated that the reef and adjacent silt-sand area provided the resources these fish needed on a daily basis. The deployment of artificial reefs over less complex sand substratum appears to be viable management practice to supplement habitat important to the red snapper population.

Acknowledgements

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